Volume II.] *February, 1901.* [*No. 5.*

BIOLOGICAL BULLETIN.

NOTES ON THE HABITS OF PYCNOGONIDS.[1]

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THE Pycnogonids constitute a small and well-defined group, especially interesting on account of their peculiar and unique structure. In general they have been largely neglected by naturalists, especially as compared with some other groups, but they have received considerable attention from specialists, and several excellent monographs have appeared dealing with their structure and classification; in fact, all the literature of the group is very largely systematic or strictly morphological. The embryology has been worked out for some forms by Dohrn and Hoek, and in this country by Morgan,[2] who has also given an extended account of the metamorphosis of Tanystylum, and considerations on the phylogenetic position of the Pycnogonida.[3] The principal systematic work in this country has been done by Wilson,[4] who described some fifteen species found on the New England coast. Practically nothing has been written on their habits, which ought, it would seem from the isolated position of these animals, to offer some very interesting comparisons with those of other arthropods. An excellent opportunity for this work was offered during the past summer at the

[1] From the Zoölogical Laboratory, University of Michigan.

[2] Morgan, T. H., "A Contribution to the Embryology and Phylogeny of the Pycnogonids." *Stud. Biol. Lab. J. Hopkins Univ.* V., No. 1, pp. 1–76. 1891.

[3] Morgan, T. H., *loc. cit.*, and "The Relationships of the Sea-Spiders," *Biol. Lect. Marine Biol. Lab.* for 1890. Seventh Lecture, pp. 142–167. 1891.

[4] Wilson, E. B. (*a*) "A Synopsis of the Pycnogonida of New England," *Trans. Conn. Acad.* V., pp. 1–26. 1878. (*b*) "The Pycnogonida of New England and Adjacent Waters," *U. S. Fish Com. Rept.* for 1878, pp. 463–506. 1880.

Marine Biological Laboratory at Woods Holl, and at the suggestion of Dr. S. J. Holmes, to whom I am also indebted for much help and advice, I undertook to ascertain something of the habits and reactions of the forms found there. The present paper embodies some of these observations, which though far from complete seem to be of interest. I hope to be able later to supplement them by a more comprehensive account of the biology of the group. Much of this work is rendered difficult by the fact that the animals are not easy to observe under natural conditions.

As has been noted by Morgan and other authors, there are three species of Pycnogonids to be found at Woods Holl, representing as many genera. These peculiar animals may be found in nearly every collection of hydroids made from the piles or dredged up from the bottom, their long legs appearing to be hopelessly tangled among the stems of the hydroid as they kick slowly about in an aimless but persistent fashion. Perhaps the commonest of these, and by considerable the largest (extent 40 mm. to 50 mm.), is the dark purple colored *Anoplodactylus lentus* Wilson (= *Phoxichilidium maxillare* of Morgan and others), which is especially abundant in colonies of Eudendrium taken from the piles. A smaller species of a yellowish color, *Tanystylum orbiculare* Wilson, measuring about 7 mm. in extent, was found fairly abundant in a yellowish hydroid almost the exact color of the Pycnogonid. Anoplodactylus was on no occasion found among the light-colored hydroid, nor did I ever find a specimen of Tanystylum among the dark colonies of Eudendrium, where Anoplodactylus is fairly inconspicuous, though I have found the latter among the much lighter colored Bugula growing near the Eudendrium. I am not prepared to say that this is a case of color adaptation, as my observations were too limited to confirm this view, but merely throw out the suggestion for what it is worth. And it is worth remarking in this connection that the third representative occurring in this locality, *Pallene brevirostris* Johnston (=*P. empusa* Wilson), which is a slender whitish or more or less transparent form and is very hard to see for this reason, was found to be much more generally distributed than either of the other species, being found among both light and dark colored hydroids and algae. Pallene impresses one as the smallest form of the three owing to its extreme slenderness, though it is really almost twice the extent of Tanystylum, measuring some 12 mm. to 13 mm. across.

Swimming and Crawling Movements.

The activities of the three species of Pycnogonids under consideration are in a way directly correlated with their structures. Tanystylum, a short-legged and compact form, is very sluggish and inert; if placed at the surface of a dish of water, it kicks hardly at all, but sinks immediately to the bottom,[1] where it does not attempt to crawl but usually draws its legs together over its back and remains quiet. Pallene, on the other hand, under the same conditions does not sink to the bottom, but by vigorous kicking movements of its long slender legs remains suspended in the water, for a considerable time at least, its further movements being determined by the conditions, one of the most important of which, as will be shown later, is light. In the actions of Anoplodactylus there is great individual variation, but in general it may be said that they are intermediate between those of Tanystylum and Pallene. Some specimens sink almost at once to the bottom, where they rest in whatever position they may strike; others may crawl along upon the sand, or partly swim, touching the sand with only the tips of certain of the legs; or still others may swim entirely free from the bottom. As with Pallene, just what the animal does appears to depend largely upon the conditions. Most of my observations were made upon Anoplodactylus, for the reason that it was easiest to obtain and of convenient size for observing the movements in detail.

Before going further it may be well to give a brief explanation of the terminology which I shall use. Various authors have used different names for the seven pairs of appendages

[1] In these experiments the bottom of the dish was covered by a layer of fine sand. The depth of water was usually about 5 cm. to 7 cm., though deeper water was tried with no difference in the results.

of the Pycnogonids, largely as they regarded them homologous to the appendages of the Crustacea or to those of the Arachnids. Dohrn obviates this difficulty by simply numbering them in their natural order, I–VII (Fig. 1).[1] For convenience I shall speak of the third pair as the ovigerous legs (these are absent in the female of Anoplodactylus), and of pairs IV–VII simply as the first, second, third, and fourth pairs of legs

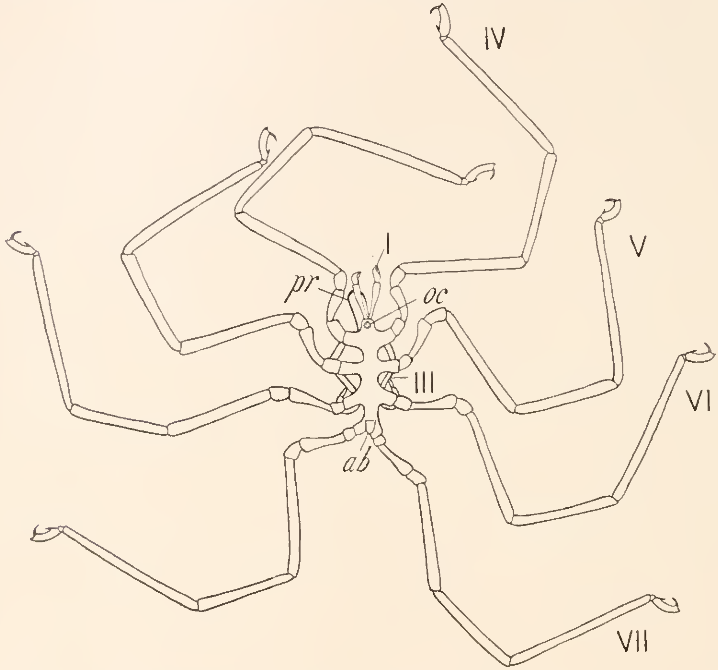

FIG. 1. — Male *Anoplodactylus lentus*, dorsal aspect: *ab.*, abdomen; *oc.*, oculiferous tubercle; *pr.*, proboscis; I, chelifori; III, ovigerous legs; IV–VII, walking legs. × 3.

respectively, or, to distinguish them from the ovigerous legs, as the walking legs. Each of the walking legs is composed of nine joints (including the terminal claw), and all four pairs are essentially alike. As may be seen by reference to Fig. 2, the first three joints in Anoplodactylus are short and capable of comparatively little motion, while the fourth, fifth, and sixth joints are long, most of the movement of the leg taking place

[1] The second pair of appendages, the "palpi," are absent in Anoplodactylus and Pallene.

in these. The articulations are so arranged that there is little chance for motion outside the vertical plane, the leg thus moving up and down in the same plane in which it extends from the body. There is, however, a possibility of movement of the leg backward and forward in the horizontal plane to a certain extent, this motion occurring chiefly in the articulation between the first and second joints. The principal movement of the leg, that is to say the movement in the vertical plane, when the animal is swimming free, is shown approximately in the diagram. Starting with the leg in the position shown at *A*, and considering only that portion distal to the third joint, the next movement is essentially a straightening out and raising

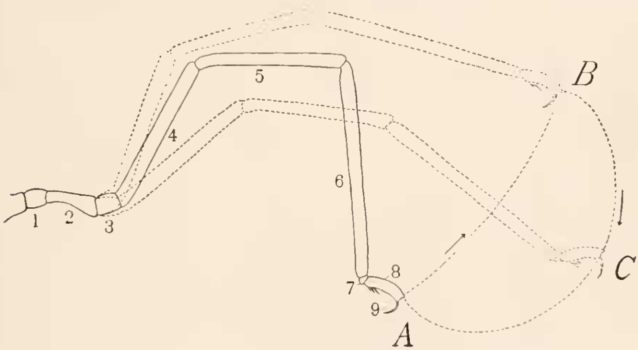

Fig. 2. — Diagram showing movement of leg in Anoplodactylus.

dorsally of that part, bringing it into a position as shown at *B*. The leg is now extended still farther and brought downward to *C*, then inward, and at the same time flexed, to the original position, *A*. This serves to indicate the movements in a rough way, and it can be readily seen that so long as the specimen is free in the water and all the eight legs are working with this same treading motion, the tendency is to propel the animal dorsalward, that is, in a direction perpendicular to its dorso-ventral plane; the fact that the legs extend radially from the body (Fig. 1) would help to keep the animal going straight in this direction, *provided they all beat with equal force*. If the claw of any leg should grasp a solid object as it comes down from *B* to *C*, the movement *C–A* would pull the animal in the direction of that object.

We are now in a position to examine more carefully the variations in the actions of the different individuals when placed in the water. As mentioned before, if the animal treads vigorously enough to overcome the force of gravity, it will swim; and so long as the body remains exactly in a horizontal position it will only move directly up or down according to the vigor of the strokes; but as soon as the body gets out of this plane the animal will progress through the water in the direction in which its dorsal surface is turned. For it to remain in a horizontal plane it is necessary that the legs should all beat with equal force; but as a matter of fact *the anterior legs beat oftener and with more vigor than the posterior legs*, thus raising the anterior end and tilting the animal backward. I did not make out any regular order of movement of the legs further than this, that the posterior legs seem to lack the vigor and strength and to be less under the control of the animal than the anterior pairs. A specimen which does not tread fast enough to raise itself from the bottom, or possibly one whose specific gravity is greater, crawls or walks straight ahead upon the sand, apparently, at first sight, much as an insect walks; but upon closer examination it may be seen that most of the movement is accomplished by the first pair of legs, assisted to some extent by the second, while the third and fourth pairs seem to be a hindrance rather than a help. By reference to Fig. 2 it can be seen how the anterior legs, by hooking into the sand, can pull the animal forward; while for the fourth pair to help in the forward movement it would be necessary for them to *push*, which would require a motion exactly the reverse of that which has been described for them when free from the bottom. Instead of this they drag along in a sort of helpless fashion, seeming to attempt the same movement as before, but hindered by striking the sand and by the forward movement of the animal as a whole due to the stronger anterior legs. A considerable backward and forward movement is now to be observed in the second and third legs, but this is probably also due to the pulling forward of the body after the legs are put down onto the sand, and not to a direct action of the legs themselves, the motion being allowed for, as before stated, by the specially arranged articulation between the first and second joints. In order to prevent the specimens from swimming while making these observations, and to force them to crawl, a small collar of tinfoil was clasped around the body between the second and third pairs of legs, care being taken that it was small enough not to interfere with the movements.

Reaction to Light.

As has been stated, one of the most important factors concerning the movements of the Pycnogonids when placed in the water is the direction of the source of light. If the dish containing them is placed near a window, the animals either swim or crawl quickly to the light side of the dish.[1] This fact has been noted by Loeb,[2] who says of Anoplodactylus : " Es ist wie die meisten frei beweglichen Bewohner der Oberfläche des Meeres positiv heliotropisch," and he also states that when the body was severed between the second and third pairs of legs, the anterior portion still reacted in the same way, while the posterior portion, which was comparatively inactive, moved independently of the light. These results were easily verified, and it was further ascertained that the oculiferous tubercle (Figs. 1 and 4, *oc.*) is the photo-recipient organ, for when this was cut off the animals failed entirely to show any response to the light. Although there are, of course, individual variations, it is surprising how quick this response usually is, especially if the dish is covered above and on the sides away from the window, so as to exclude all light from other directions. In the diffuse light three or four feet from a northwest window, lively specimens usually traveled an average of 12 cm. to 15 cm. in thirty to forty seconds. The response seems to be more pronounced when the light enters horizontally.

In moving towards the light the animals may adopt any one of the modes of locomotion previously described : (1) they may

[1] This is not the case if there are hydroid stems or similar objects which the Pycnogonid can grasp. The tendency to cling to anything of this character seems to be stronger than the reaction to light.

[2] Loeb, J., " Bemerkungen über Regeneration," *Arch. Entwick-Mech.* Bd. ii, pp. 250–256. 1896–97.

swim entirely free; (2) they may partially swim, kicking along on bottom with those legs that are down; or (3) they may crawl with all the legs on the bottom. The second method is the most common and the one in which the greatest speed is made. But the striking thing to be noticed is that in the first and second methods, those in which they swim or partially swim, the movement is backwards, or nearly backwards, while in the third method of locomotion, when they crawl on the bottom, they invariably go straight ahead, that is to say, with the anterior end directed towards the source of light. It thus appears that in moving towards the light they orient themselves differently, according to whether they swim or crawl; and, as I have shown, whether they swim or crawl depends directly upon the vigor or *rate* of the treading movement and not upon any difference in the *direction* of the stroke. The question naturally presents itself, Why should there be this difference in orientation in the two cases? In order to determine this, let us first consider specimens which are forced to crawl by being weighted with tinfoil. If an animal so weighted is placed in the water with its anterior end towards the light, it crawls directly ahead without turning; if its head is pointed in any other direction, it gains this same orientation by making a short circle, turning in the shortest direction towards the light. Now for any animal to walk in a circular path it is necessary for those legs on the outside of the circle to act with a greater force than those on the inside, and thus shove the body around; in the case of an animal orienting itself so as to head towards the source of light, this means that *those legs away from the light act stronger than those towards the light*, they being the legs on the outside of the circle which the animal describes in coming around. If this rule holds true when the Pycnogonid swims, and I see no reason why it should not, we have a simple explanation of its orientation with reference to light at all times. This can perhaps best be made clear by taking a particular case and following it through. An animal is placed on the bottom with the long axis of the body at right angles to the rays of light. This is represented in the diagram *A* (Fig. 3), in which we are supposed to be looking at one end of the Pycnogonid as it rests upon the sand. The arrow indicates the direction of the light. The animal at once begins to kick and the body is raised from the bottom, but since those legs on the side from the light (*a*) beat stronger than those towards the light (*b*), that side is raised more and the body is tilted so that the rays of light strike approximately perpendicular to the dorsal surface, as shown in *B*. Since the regular movement of the legs tends to propel the animal dorsalward, it moves toward the light. And now the fact that the anterior legs beat more efficiently than the posterior must be taken into account; this action tends to bring these legs uppermost, that is, around to the place of the legs (*a*) in diagram *B*. This is shown in *C*, where we see the animal from the side instead of endwise, as in *A* and *B*; in this position the posterior legs kick along on bottom. As a matter of fact the anterior legs seldom come entirely around so as to be directly uppermost, but only approximate that position, the third and fourth legs of one side or the other being the ones to touch bottom rather than the posterior legs; so that the animal does not move directly backwards but rather "cornerwise." If the movement is more vigorous, or if the light comes more from above, the animal may raise itself entirely free from the bottom, keeping, however, the same relative position.

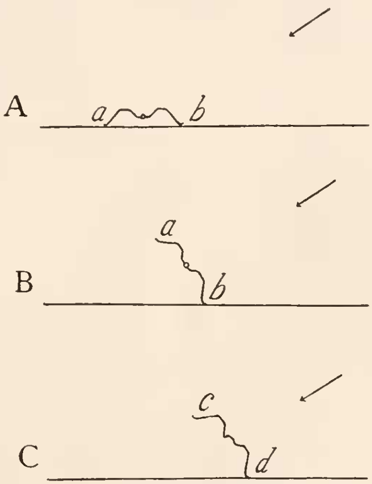

Fig. 3. — Diagram representing the reaction of Anoplodactylus to light.

If the orientation is different from the case given, it is easy to see how the same result is brought about. In a case where the animal is headed directly from the light, the anterior end has but to raise from the bottom to bring it into this position; and in the other possible case, when the head is directed towards the light, although the movements may be indefinite at first, it soon gets out of direct orientation and then turns around the shortest way, as in the first case.

Pallene shows even a more marked positive phototaxis than Anoplodactylus. If the light comes in nearly horizontally, it usually tilts over to an angle of about ninety degrees, or until the body is nearly perpendicular to the bottom, and moves quickly towards the light by a rapid movement of the legs. Pallene is much the better swimmer of the two and seldom moves along the bottom in the manner described for Anoplodactylus. So far as I could make out, the leg movement is exactly similar in the two species.

Transfer of the Eggs.

During the latter half of August the males of Anoplodactylus may often be found bearing the egg-masses upon their ovigerous legs. As a general rule, among Pycnogonids the eggs are gathered into little spherical or spheroidal balls strung along on the ovigerous legs, but in Anoplodactylus they are in more or less irregular masses through which both of the ovigerous legs pass (Fig. 4); their white color in this form, clearly offset by the dark body of the animal, gives them much the appearance of little bunches of wet cotton. Sars[1] says of the genus, evidently basing the statement on *A. petiolatus*, that there are "several globular egg-masses attached to the false legs in the male," and in his figure of this species there are five such masses shown on the right ovigerous leg. It is possible that in *A. lentus* the irregular masses may later

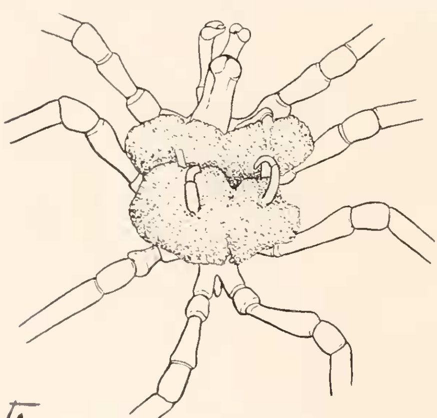

FIG. 4.—Male *A. lentus* from right side; walking legs removed. Reference letters as in Fig. 1.

[1] Sars, G. O., "Pycnogonidea," *The Norwegian North-Atlantic Expedition, 1876–78. Zoölogy*, vol. vi, p. 25, and Pl. II, Fig. 2 *b*. 1891.

roll up into separate balls, for I have had opportunity to observe them for only a few days after they were laid; but this does not seem to me probable.

Cases of the males carrying the eggs are rare among animals and occur in widely separated groups; the male of the obstetric toad (*Alytes obstetricans*) winds the egg-strings about his body and carries them till the tadpoles hatch; the male of a South American frog (*Rhinoderma darwinii*) takes the eggs into his vocal sacs to develop; and the males of some of the Lophobranch fishes have brood pouches for the reception of the ova. In looking over the literature I have been unable to find any reference to this habit among the invertebrates, aside from the whole group of Pycnogonids. It seemed a matter of considerable interest to know just how such a seemingly intelligent act as the transfer of the eggs to the male takes place in animals whose movements in general seem to exhibit so low an order of psychic development, and I kept close watch of them with this point in view. So far as I am able to ascertain, the process has never been described, though Hoek[1] gives an account of the copulation in a European species as follows: "In regard to the way in which the eggs are laid, I had the good fortune to observe the copulation of a male and female *Phoxichilus laevis* Grube, when I was, last summer, in the zoölogical station of Professor H. de Lacaze-Duthiers at Roscoff. The eggs are fecundated the moment they are laid, and the copulation, therefore, is quite external, brought about by the genital openings of the two sexes being placed against each other. Half an hour after the beginning of copulation, the male had a large white egg-mass on one of his ovigerous legs, and about one hour later both masses were present." Only once, on August 16, at 6.15 A.M., was I fortunate enough to observe the pairing of Anoplodactylus. When first noticed both animals were among the hydroids; the male was clinging to the dorsal surface of the female and headed in the same direction. Both animals were kicking slowly in an indefinite sort of way, but gradually the male drew forward and,

[1] Hoek, P. P. C., "Report on the Pycnogonida, dredged by H. M. S. *Challenger* during the years 1873-76," *Challenger* Reports. *Zoölogy*, vol. iii, p. 131.

passing down over the anterior end of the female, came to lie beneath her, the animals being now headed in opposite directions and with their ventral surfaces opposed. The basal joints of the legs of the female were approximated below, with the mass of eggs between them. As the male came around below the female, the ovigerous legs, which are curved at the ends, forming a sort of hook (Fig. 5), fastened into the egg-masses, and as the animals separated pulled the eggs away with them. The masses did not pull away clean, but strung out more or less, leaving a very few eggs still on the female. For some time after they separated the male was observed to work the ovigerous legs slowly, the effect seeming to be to get the eggs more firmly upon them and into a more compact shape. The time from when the animals were first observed until they had separated was only about five minutes.

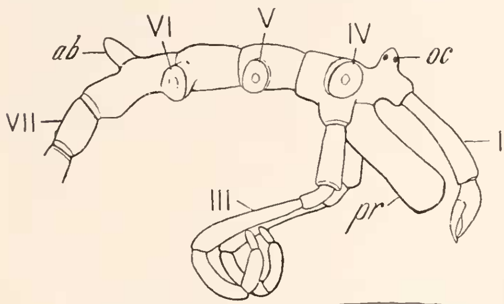

FIG. 5. — Male *A. lentus* from below, showing egg-masses on the ovigerous legs. Fig. 4.

Some of the males have but one egg-mass on the ovigerous legs, but more often there are two, as shown in Fig. 4. I am unable to say with certainty whether this means that the male takes the eggs from two females or that he gets them in two masses from one; but from the fact that in those cases in which they were examined the eggs in the two masses appeared to be in the same stages of development, I am inclined to the latter view. The genital openings are situated on the ventral side of the second joint of all four pairs of legs, and it is easy to see how the eggs of one female might gather into more than one mass.

Summary.

1. The three forms treated are more or less adapted in color to their several habitats.

2. Swimming is accomplished by a treading movement of the legs, which tends to propel the animal dorsalward.

3. The stroke of each of the legs is the same in character, but is stronger in the anterior legs than in the posterior.

4. Crawling is accomplished by the same action of the legs as swimming, when the action is not strong enough to raise the animal from bottom. The anterior legs are most effective, pulling the animal forward; the action of the posterior legs is a hindrance.

5. Both Anoplodactylus and Pallene are strongly positively phototatic.

6. In *crawling* towards the light the animal proceeds with the anterior end in advance. If not oriented in this direction at first, it becomes so oriented by making a short circle, in every case towards the light. This means that those legs away from the light beat stronger than those towards the light.

7. In *swimming* towards the light the animal moves approximately backwards, with the anterior end somewhat raised. The amount it raises depends upon the activity of the individual and the slant of the rays of light.

8. This orientation is accomplished by the same actions that produce orientation when crawling, except that they are more vigorous, raising the animal from the bottom.

9. The transfer of the eggs from the female to the male is a comparatively simple process.

Ann Arbor, Mich., Nov. 23, 1900.